The Development of the Vascular Structure of Dianthera americana L.[1]

DISSERTATION

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W. RALPH JONES

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THE DEVELOPMENT OF THE VASCULAR STRUCTURE OF DIANTHERA AMERICANA

W. RALPH JONES

(WITH PLATES I–IV)

In 1907, THEO. HOLM (5), in describing the anatomical structure of *Dianthera americana,* called attention to the "polystelic" condition of the stem. This paper seems to be the only one ever published on this intensely interesting plant. So at the suggestion of Professor DUNCAN S. JOHNSON, I have made a study of the ontogenetic development of the stelar structure in order to find out how the "polystelic" condition of the mature plant is derived.

The material studied consisted of seedlings grown in the laboratory and greenhouse from seeds collected near the Chain Bridge (over the Potomac River about four and one-half miles above Washington, D.C.), of seedlings collected at the Chain Bridge, and of mature plants from Chain Bridge and from near Betterton, Md.

Most of the material studied was imbedded in paraffin, and sectioned 5–10 μ thick. Various stains were used, but the best results were obtained with methyl green and acid fuchsin.

Dianthera americana is a perennial herb, with an erect stem 3–9 dm. high, grooved and angled, usually simple, and having opposite, simple, linear-lanceolate leaves 75–150 mm. long and 6–15 mm. wide. At the Chain Bridge, the plant grows in the tide pools on the rocky flats on the north side of the river, and also along the banks of the Chesapeake and Ohio Canal, which at this point runs parallel to the river just back of the flats. The plant produces flowers from May on through the summer, ripening its fruits from

about the middle of July to the end of summer. The fruit, a loculicidal two-celled capsule, dehisces violently, often throwing the four seeds a distance of several decimeters. The seeds germinate very soon after being shed, the seedlings reaching a height of about 2 dm. by the end of the growing season. Branches formed in the axils of the basal leaves, and at first growing upward, soon curve, and grow downward to just below the surface of the water, then take a nearly horizontal direction. These stolons, becoming 0.5–1 dm. long, send out adventitious roots at the nodes that pass downward into the mud.

At the end of the growing season, the vertical shoot dies down to just below the usual level of the water, usually to the top of the first node below the surface. The rest of the stem remains green and apparently in good condition for some time, but gradually rotting. The stolons, with their scalelike leaves, where exposed to the light, remain green throughout the winter, as do also the upper parts of the adventitious roots. In the spring, the terminal bud of the stolon again starts its activity, turning upward, and sending up a vertical shoot into the air. This shoot develops elongated leaves, and rarely branches from near the base. The basal buds, however, usually produce the rhizomes by means of which the plant perennates. Buds formed in the axils of the upper leaves develop into the capitate-spicate inflorescences of violet or nearly white flowers.

At Betterton, Md., the plant grows under different conditions. Instead of growing in the water, it grows in the sand just above the level of high tide; the rhizomes grow about on the level of the top of the moist sand, the lower one to three internodes of the aerial shoot being buried in dry sand. The basal branches grow upward a few centimeters, turn down, and then become horizontal, growing along the top of the moist sand at a depth of 5–10 cm. below the surface. The basal part of the erect shoots and also the rhizomes, therefore, are without chlorophyll. Although many discharged capsules were seen, I could find no trace of seedlings, so I cannot say that the life-history here is the same as at Chain Bridge, but from the time of flowering and of the ripening of the seeds, and from the general habit of the plants, I see no reason for believing that there are any marked differences in the general life-history.

As HOLM (5) has pointed out, both the vertical aerial stem and the horizontal submerged rhizome show, in a cross-section of an internode, six peripheral and one central bundle, each of leptome, hadrome, and pith, and each completely surrounded by a thin-walled endodermis, each having, therefore, the appearance of a complete stele (fig. 8). For this reason, HOLM says that the plant is polystelic; from its development, however, it will be seen that it is really astelic.

At each node there is a fusion of the six peripheral meristeles to form a complete ring of vascular tissue, which breaks up in a very regular way to form the six peripheral meristeles of the internode above (fig. 1). Each of the bundles of the lower internode divides at the node to form a Y; then each branch fuses with a branch of the adjacent Y, thus giving rise to the six peripheral bundles of the next internode. The single leaf traces join the vascular system of the stem at the crotches of two opposite Y's. The two bundles which supply the traces are usually, though not always, larger than the other four. There is also a connection made, at each node, between the central bundle and the peripheral ring of vascular tissue by means of a transverse arm, coming out from the central bundle at right angles to it and fusing with the vascular ring just below the insertion of the leaf traces (figs. 3–8 show a series of transverse sections through the node). The structure of the node next above or next below the one described is exactly the same, except that its plane of symmetry is at right angles to that of the adjacent one, as is shown in fig. 1. A diagram of the path of the bundles in a mature plant is shown in fig. 2.

The seeds

The seeds (figs. 11 and 12) are much flattened, and are nearly circular in outline. They are about 2–3 mm. in diameter, and about 0.75–1 mm. in thickness. On the lower side the edge of the seed is slightly hollowed out to form a pocket in which lie the hilum and the micropyle. The testa is brown in color, and has a much roughened surface, owing to the distortion of the underlying cells, of which there are two to four layers (fig. 10). The walls of the epidermal cells are thickened in bands which fuse at some places, and at others taper to a point and disappear. The inner

cells are thin-walled, and are much distorted in shape. The endosperm is represented by a thin pellicle, usually two cells in thickness, except at the lower edge of the seed, where it thickens to form a mass of appreciable thickness, which forms a cap over the free end of the hypocotyl. The well developed embryo nearly fills the seed. The two large cotyledons are flat, nearly circular in outline, accumbent, the curved hypocotyl lying closely against the edges of the cotyledons, and being free only at the end. The seed, therefore, corresponds very closely to that of *Dianthera nodosa* Benth. & Hook. as described by SCHAFFNIT (**8**, p. 65).

The epidermis of the hypocotyl is composed of small cells which are elongated vertically. The cortex consists of about ten layers of cells, radially arranged, and of larger diameter than those of the epidermis. They are flattened vertically, and appear nearly square in cross-section. The innermost layer appears in no way different from the rest of the cortex. One striking feature of this layer, however, is the division of its cells, on each side of the central cylinder between the protoxylem poles, to form two layers (fig. 14). Schizogenous air cavities, of small diameter, but of considerable length, have already formed between the angles of the adjoining cells.

The central cylinder is sharply marked off from the surrounding cortex, owing to its greatly elongated cells of very small diameter (fig. 14). Just below the insertion of the cotyledons, the central cylinder divides to form the two procambial cotyledonary traces (fig. 13).

Germination

The earliest stages of germination have not been observed in the field. Seeds brought into the laboratory and soaked in water swelled about 0.5 mm. in diameter and about 0.25 mm. in thickness. These soaked seeds were then placed in a moist chamber, either on wet filter paper or on wet sand. The testa soon split, the hypocotyl pushing through. Further growth now forces upward the upper end of the hypocotyl and the cotyledons, often carrying the testa still clinging to one or both of the cotyledons. The latter soon become green, continue their growth, and function photosynthetically for some time. The plumule is rather tardy in starting its growth.

For ease of description, we will divide the growth of the seedling into stages corresponding to the number of pairs of leaves present.

STAGE I

The first seedling stage (fig. 15) shows the elongating hypocotyl well out of the testa, pushing upward the cotyledons which are frequently still inclosed within the testa. All the endosperm found in the seed has been used up. The primordia of the first pair of leaves are beginning to develop, but no sign of differentiation of the foliar traces has yet appeared. From each cotyledon one double bundle enters the hypocotyl (fig. 16). These bundles approach each other, and very soon come together to form the central cylinder.

In the middle of the hypocotyl, a cross-section shows an epidermis of cells slightly elongated radially, the inner and side walls thin, the outer walls slightly cutinized; the cortex, about 10–12 cells in thickness, the outer two or three layers of irregularly arranged cells, which are beginning to show a slight thickening and later forming a typical collenchyma. The remaining inner layers of the cortex are made up of rounded thin-walled cells, very regularly arranged in radial rows, their walls being in contact except at the angles, where there are formed small schizogenous air cavities, which latter extend vertically for a considerable distance. The innermost layer of the cortex is not modified in any way, being like the other cells of the inner part of the cortex in size, shape, and content of cells.

The central cylinder, or stele, is very sharply marked off from the surrounding cortex, being made up of much smaller cells except at the very center. The pericycle is of one layer except opposite the xylem poles, where it is of two layers. The xylem is arranged in two opposite groups, the protoxylem being exarch. The four phloem groups are placed one on each side of the xylem poles. The rest of the central cylinder is of thin-walled parenchyma, small near the periphery, but becoming much larger at the center. There are no air spaces in the central cylinder.

Transition.—In the petiole of each of the cotyledons is a double bundle, the protoxylem of which occupies an endarch position. As the two bundles of the cotyledons enter the hypocotyl, there is

a rotation of the xylem, the protoxylem becoming exarch. On reaching the transition region, near the base of the hypocotyl, the phloem of each bundle divides, and passes to the right and left of the xylem. Each half moves to the side of the stele, finally fusing with a half of the phloem from the other bundle. This forms a typical diarch root, the transition being that of Type III of VAN TIEGHEM. Fig. 17 shows a diagram of the path of the vascular tissue at this stage.

STAGE II

In the second stage, the first pair of leaves have enlarged sufficiently to be seen easily by the naked eye (fig. 19). The primordia of the second pair of leaves are not differentiated until near the end of this stage. The bases of the cotyledons have fused to form a short tube. The leaves of the first pair are opposite and are decussate to the cotyledons. As they develop, there begins the differentiation of a single vascular bundle for each, the differentiation beginning at the node, passing outward into the leaf, and downward into the stem, passing through the very short epicotyl into the hypocotyl, and becoming inserted between the cotyledonary bundles, the protoxylems finally disappearing near the base of the hypocotyl.

There have also started to develop two buds, one axillary to each cotyledon, but at this stage neither shows any differentiation of vascular tissue. A diagram of the course of the vascular tissue at this stage is shown in fig. 18.

The cortex and epidermis are very nearly as in the preceding stage, the angles of the outer cortical cells being more thickened, however, and the outer wall of the epidermal cells being heavier than before. Glandular hairs of the type found on the mature plant (figs. 26 and 27) are numerous on the hypocotyl and cotyledons.

At the close of this period of development, a bundle develops on each side of the stem between the two traces of the first pair of leaves. These bundles, at the lower end, are forked just over the cotyledonary traces, the forks being inserted on either side of the traces, between them and the bundles from the first leaves. At the upper end, the bundles fork, the branches passing off nearly

at right angles to the main bundle, and being inserted on the sides of the leaf traces of the first pair of leaves. There is thus formed a complete ring of vascular tissue in the first epicotylar node. Rarely the forks at the base of the bundles are of very unequal size, or one of the bundles may even fail to divide, in this case merely bending aside, and becoming inserted on one side or the other of one of the cotyledonary traces. The direction of differentiation of these side bundles seems to be acropetal, but this could not be made out definitely. The cross-arms connecting the bundles with the traces of the first pair of leaves, however, are undoubtedly younger than the main part of the bundles. Fig. 20 shows the course of the bundles at this stage.

STAGE III

With the development of the second pair of opposite leaves at right angles to the first pair, and directly over the cotyledons, we have the third stage (fig. 22). At the insertion of each of these leaves, there starts to differentiate a single bundle, passing outward into the leaf, and downward through the stem, becoming inserted in the crotch of the fork of the bundle just developed at the close of the preceding stage (fig. 21).

If we now examine this latter bundle (fig. 23), we find that it possesses three protoxylem elements, one being derived from the newly developed trace of one of the second pair of leaves, the other two connecting, one through each of the horizontal connecting branches, with the outgoing leaf traces of the first pair of leaves. At the lower end of the bundles (figs. 24 and 25), one of the protoxylems passes out along one of the forks; the other two, which have been closely applied to each other throughout the whole length of the bundle, pass out the other. These bundles at first have the appearance of being double, the two parts being separated by a narrow parenchymatous (medullary?) ray, but being, later at least, entirely surrounded by a complete endodermis.

A cross-section (fig. 28) through the middle of the second epicotylar internode shows an epidermis, or rather protoderm, of thin-walled cells, sharply marked off from the internal cells. Within this protoderm is a meristematic tissue of cells practically all alike, showing no differentiation into cortex and central cylinder,

and with no air spaces. In this ground tissue are imbedded the two procambial strands of the traces of the second pair of leaves.

In the middle of the node below, there is to be seen a ring of vascular tissue inclosing an area of rounded parenchymatous cells similar in appearance to the cortical cells surrounding the vascular tissue. The inner layer of the cortex differs from the remaining cortical cells only in being more tightly placed together, thus forming a sheath. There is as yet no thickening of the walls of the cells forming this sheath.

Immediately below this node, the sheath sinks in between the four bundles, breaks, the ends turn in and form a complete sheath around each of the bundles, inclosing also a small amount of the undifferentiated parenchyma (pith?) on the inner face of each bundle. This condition persists throughout the internode. At the forking of the two opposite side bundles (figs. 24 and 25), the sheath sinks in between the forks, and so forms a complete sheath around each branch. On entering the cotyledonary node, these sheaths break on the inner face of the bundles, open out, the ends of each fuse with those of the adjacent bundles, forming thus a complete, but at first irregular, sheath around the entire central cylinder of the hypocotyl, which sheath continues downward into the root. At places, the bundle sheaths in the basal epicotylar internode show the characteristic Casparian dots on the side walls; this is also true of the sheath around the central cylinder of the hypocotyl and root. At this stage, however, the sheath is extremely irregular, being often of two layers for a short distance, and in most places showing no special endodermal characteristics.

A cambium has appeared in the bundles from the first pair of leaves, but very little secondary tissue has as yet been formed. In the hypocotyl there is a much interrupted cambium which has formed a little secondary tissue. At a later stage, the cambium forms a complete ring, and so develops a complete ring of secondary vascular tissue. In the root there is now to be found an interrupted cambium, which later becomes complete except at the protoxylem poles. The older primary root, therefore, will have two crescent-shaped masses of secondary tissue, the horns of which come together opposite the protoxylem poles.

The buds, found at the preceding stage in the axils of the cotyledons, have developed somewhat, each having now two very small leaves, each of which furnishes a single trace which passes downward into the hypocotyl. These become inserted, one on each side of the cotyledonary trace, between it and an arm of the forked bundle entering from above.

The bases of the first pair of leaves were at first distinct, but they have by this time grown together to form a short tube. This is the case with all the later formed leaves. A bud is starting to develop in the axil of each of the first pair of leaves, but at this stage has developed no vascular tissue.

From now on, the order of differentiation of new bundles is the same as that just described. At the close of each stage, there develops a pair of opposite bundles, each double in appearance, having two groups of protoxylem and protophloem elements separated by a parenchymatous ray. These bundles fork below, the forks being inserted between the traces of the underlying pair of leaves and those of the latest formed pair. Above, the bundles fork, connecting with the outgoing, latest formed leaf traces. In the next stage, these bundles become surrounded by a sheath which finally develops into a well marked endodermis. At the beginning of each stage, there is differentiated a trace from each of the newly formed leaves, which trace passes downward to the node below, being there inserted in the crotch of the underlying forked bundle which has just been developed at the close of the preceding stage.

The central bundle

The earliest sign of any medullary vascular tissue is to be found in a single example of a fourth-stage seedling, where, in the first epicotylar node, there are traces of medullary phloem. The course and attachment of these medullary phloem strands (fig. 30) are best described by starting with the conditions found just below the node, and following these upward through the node.

As the four bundles found in the basal epicotylar internode spread out on entering the node to form a complete ring, three protophloem elements from the peripheral vascular tissue pass inward toward the center. One of these protophloems arises from

the side of one of the leaf traces of the first pair of leaves. This single protophloem element passes inward toward the center of the ring. It never reaches it, however, but turns upward, and disappears in the middle of the node. The other two protophloem elements arise, one from the side of the other leaf trace, and the second from the adjacent face of one of the side bundles. These pass toward the center, become applied to each other, and pass vertically upward for a short distance; one disappears, the other soon turns, and passes back to that side of the stem on which it arose, becoming inserted, at the top of the node, on one of the "forks" on the side nearest one of the descending traces of the second pair of leaves.

In a very similar case found in a fifth-stage seedling, a single protophloem passes off toward the center from each side of each leaf trace. These four protophloem elements pass toward the center and turn upward, then turning back to the ring, each fuses with one of the descending forks, just as these enter the ring at the top of the node. In these two cases, the medullary vascular tissue is all entirely intranodal, there being no trace anywhere except just within the one node.

In the fifth stage, however, there is usually developed the central bundle of both xylem and phloem, passing from one node to the next. There is considerable irregularity in its formation, some of the fifth-stage seedlings being entirely without any medullary vascular elements. Taking a seedling where the central bundle has developed, we find, at the third node back from the apex, an elliptical vascular ring surrounded by a well marked sheath which usually, at this stage, does not possess any special endodermal characters. There is no sign of any internal endodermis in this node.

In passing downward out of this node, just as the vascular ring breaks up into four bundles, from one edge of one of the side bundles, a small group of phloem and xylem elements passes inward, free from the outer ring, to the center of the pith, meeting there another group of vascular tissue, which has broken off from the other end of the same side bundle. At a more mature stage, the medullary bundle may be derived from four sources, one at each end of each of the side bundles.

At this stage, the oblique cross-arms are imbedded in the parenchymatous tissue, there being no trace of any sheath. After turning so as to pass vertically downward, the fused bundles become surrounded by a more or less well marked sheath, which soon shows the characteristic Casparian dots on the side walls of the cells. Just above the node below, most of the vascular elements have died out, there being left only three or four phloem elements. These lose their surrounding sheath, and pass across to the peripheral vascular bundles at a level where the endodermis surrounding the forks has just broken. The medullary vascular tissue becomes applied to the outer side of one of the forks, on the opposite side of the stem, however, from which it branched off at the node above. Soon after this the nodal ring becomes closed. If we examine closely the upper node, we find that the vascular elements which turn in to form the central bundle may be traced through the node into the forks of the side bundles of the overlying internode.

At the next stage, the central bundle is differentiated in the next internode above in the manner just described, the lower end of this new bundle becoming inserted at the top of the older central bundle between the incoming cross-arms. A cambium makes its appearance in the central bundle and cross-arms about two stages after the differentiation of these bundles. This cambium frequently forms a more or less complete ring. Usually, however, in the seedling stages, the primary xylem and phloem crowd over to one side of the bundle, the cambium coming in as an arc, forming a collateral bundle of exactly the same structure as the peripheral bundle, in spite of its entirely different origin.

The internal endodermis

In the first five stages, the endodermis which surrounds the bundles throughout the internodes disappears from the inner faces of the bundles on reaching the nodes, leaving only an endodermal sheath surrounding the vascular ring in the node. From the sixth stage on, however, it is usual for the endodermis to be continuous through the node, both externally and internally.

Taking an older node as a type, we find (fig. 3), just above the node, that every bundle is surrounded by a regular endodermal sheath. The leaf trace sheath is usually well differentiated only

on the abaxial side. The sheaths of the two bundles between which the leaf trace enters soon open, the ends becoming connected so as to form a complete sheath around the two bundles and the leaf trace (fig. 4). The inner face of the sheath now bulges toward the central bundle, finally coming in contact with it, and breaking at the point of contact, thus forming a continuous sheath inclosing a dumb-bell-shaped area, each head consisting of the leaf traces and the two side bundles of the stem, the central bundle in the middle of the connection. The endodermis on each side of each "head" now bulges toward the remaining pair of stem bundles, coming in contact with the endodermal sheaths of the latter, and breaking at the point of contact.

There are thus formed three complete rings of endodermis (fig. 5), one externally surrounding the vascular ring, the other two internal, one on each side of the transverse connecting arms. These connecting arms very soon break, the endodermis sinking in so as to form one sheath around the central bundle, and another lying just internal to the vascular ring (fig. 6). This vascular ring now breaks into four parts, the endodermis sinking in until the external and the internal sheaths meet, then breaking apart, thus forming the four bundles of the lower internode, each surrounded by a complete endodermal sheath (fig. 9).

Late stage of seedling

As has been said, the seedling, by the end of the growing season, attains a height of about 2 dm. Such a plant (fig. 31), possessing about 20 nodes, looks very much like a plant of the "mature" type, but is smaller than the mature plant, and of course differs in not having arisen from a rhizome. At the base, several of the axillary buds have developed to form short, nearly horizontal branches, the rhizomes. At the very base there is a cluster of four strongly developed adventitious roots, nearly surrounding the primary root, which is still less developed than the adventitious roots.

A histological examination shows that the vascular system has developed in the manner already described. The uppermost pair of leaves furnish a single trace each; these pass downward to the

second node, where there has been formed a vascular ring. On passing through this node, we now find a new condition. Instead of the vascular ring breaking into four bundles, two of which fork lower down in the internode, it breaks into four bundles, two of which almost immediately divide, the four forks behaving in the same way, however, as the forks produced at the lower end of the internode of earlier stages (see diagram of path of bundles, fig. 29). This condition is very nearly that which exists in the apex of a mature plant (compare diagram, fig. 2), where the nodal ring breaks up immediately into six bundles, four of which, corresponding to the two forked side bundles, are usually smaller than the other two.

An examination of the lower internodes of this stage (fig. 29), or of the corresponding internodes of the intermediate stages, shows that there is a tendency from the very first for the side bundles to fork at a slightly higher level in each succeeding internode. In the third stage, where these side bundles first come in, there is but a very small amount of parenchymatous tissue inclosed above the leaf traces by these forks, forming small leaf gaps. At each succeeding stage, these gaps tend to be longer when formed. I say tend, for there is considerable irregularity. One of the side bundles may fork about the middle of the internode, while the opposite side bundle of the same internode may not fork until very near the bottom of the internode, or, as before mentioned, may not even fork at all. In any individual seedling there is a gradual transition from the immature seedling condition found in the earliest stages, and hence lowermost internodes, to the nearly mature conditions found in the uppermost internodes of the seedling at the end of the growing season.

The old seedling shows, therefore, a permanent record of its ontogenetic development, slightly obscured, it is true, by secondary thickening. It is comparable in this respect to a fern "seedling," the earliest formed internodes showing the simple (primitive?) type of structure, the later formed ones showing a gradual transition to the mature type. It must be remembered, however, that in the fern, when the mature structure is once formed, the main axis continues its growth, each succeeding internode having the mature

structure. In *Dianthera americana*, on the other hand, the main axis seems never to produce a perfect mature type, but only approaches it. The mature type is here first produced in a branch, the rhizome. When once attained, however, it is persistent, as in the case of the fern.

Owing to the secondary development of vascular tissue, the general appearance of the bundles, or meristeles, has changed considerably. Instead of being strictly collateral, as they were in the earlier stages, there is a tendency for them to become concentric, the xylem and phloem being formed on the sides, and later, by the extension of the cambium, they are also formed on the inner face of the meristeles. The cambium may even form a complete ring, though this is not common in the seedling stages.

The presence of this internal, and of course, inversely oriented mestome, causes the node of an older seedling to have a rather different appearance from that of the young seedling. On entering the node (figs. 3–9), part of the vascular tissue on the sides of the meristeles, sometimes of the phloem only, sometimes of both xylem and phloem, passes around to the inner face, becoming inverted during the passage. Part of the internal mestome of two of the bundles turns into the transverse arm, and so connects with the central bundle. Below the transverse arm there are three concentric rings of endodermis, one external to the complete ring of normally oriented xylem and phloem, the second just within the inversely oriented mestome. The third and innermost endodermis surrounds the central cylinder. The normally oriented mestome is separated from the inverted vascular tissue by a layer, several cells in thickness, of closely packed parenchymatous cells. This layer is continuous with the parenchyma of the individual meristeles, above and below the node. The middle endodermis is separated from the innermost sheath by a layer of cells continuous with the ground tissue of the internode, but much more closely packed together. There is, however, still a considerable amount of air space.

The epidermis and ground tissue of the late seedling are exactly like those of the mature plant. As HOLM has already accurately described and figured these tissues, nothing more need be said of

them. The leaves of the seedlings correspond very closely to those of the mature plant. The latter have been fully described by HOLM. One correction must be made, however. HOLM says (5, p. 326) "collenchyma and stereome seem to be entirely absent from the lateral portion of the blade," apparently overlooking the marginal strand of collenchyma occuring in both seedling and adult leaves (fig. 32).

The axillary buds

It has already been mentioned that buds are usually formed in the axils of the leaves. In most cases, except at the base of the plant, these buds, after having developed one or two pairs of very small leaves, remain dormant. Several of the basal buds may develop, giving rise to the horizontal rhizomes, by means of which the plant perennates. The bud arises as a small mound of tissue in the axil of the leaf. On this mound there soon appear the primordia of a pair of opposite leaves, whose plane of symmetry is at right angles to that of the subtending leaf. A single leaf trace from each leaf is differéntiated, and passing downward becomes inserted between the trace of the subtending leaf and an arm of the forked bundle of the stem.

As in the main stem, the next step in development is the differentiation of a pair of forked bundles, the forks of the outer bundle being inserted between the first pair of leaf traces and the trace of the subtending leaf. The arms of the other forked bundle become inserted behind the first pair of leaf traces, between them and the forks of the stem bundle. As in the stem, a pair of traces from the second pair of leaves now differentiate, and become inserted in the crotch at the top of the forked bundles. By this time it is seen that a very irregular sheath is forming around each of the bundles of the lower part of the bud (fig. 33). On entering the node below, these sheaths open on the inside, the ends connecting so as to form a complete sheath surrounding the bundles of the bud and the trace of the subtending leaf (fig. 34). Lower down, this sheath opens on the inside, the ends connecting with those of the opening sheaths of the "forks" of the stem. This forms a complete sheath around all of the bundles, as is shown in fig. 35. The endodermis now behaves in the way already described in a node which had no bud.

The later development of the axillary bud is exactly the same as that of the main stem, with this exception: while in the stem the transition from seedling structure to the mature type is very gradual, the transition in the branch is much more rapid, being completed in about 6–8 internodes. After having once been attained, the mature type recurs constantly in each succeeding internode.

Roots

In the old seedling there are to be found four types of roots, each having its characteristic structure. These are the primary, secondary, and adventitious roots, and the branches of the latter.

The primary root is diarch, maintaining this type of symmetry even when mature. Its growing point is of the "*Helianthus*" type, having distinct plerome and periblem initial groups, while the calyptrogen and dermatogen have a common group of initials. As the root matures, a cambium develops in a ring, broken opposite the two protoxylem poles, forming two crescents of secondary vascular tissue. The stele is surrounded by a sharply defined thin-walled endodermis with Casparian dots. The cortex and epidermis correspond to those of the adventitious roots of the mature plant, sufficiently described by HOLM. He, however, wrongly calls these roots "secondary" (**5**, p. 319).

The true secondary roots, that is the branches from the primary root, possess the same type of growing point as the primary root. The symmetry varies with the age, the younger parts of these roots being usually diarch, and becoming later tetrarch or pentarch. The general structure of these mature secondary roots is that of the adventitious roots. The adventitious roots, formed at the base of the seedling, and the branches of these adventitious roots, are exactly like those described by HOLM for the mature plant. These also possess the "*Helianthus*" type of growing point.

Abnormalities in the internal structure

One very striking feature about the seedlings of *Dianthera americana* is their extreme variability. Two seedlings of the same stage, that is with the same number of leaves developed, may show very great differences in the degree of differentiation of vascular tissue, cambium, endodermis, etc. For instance, a seedling of the

fifth stage may have a better developed endodermis in its basal internode than can be found in an ordinary seedling of the eighth or ninth stage.

One of the most striking abnormalities, however, is the failure of an entire bundle to differentiate. This is frequently the case with the central bundle. This may develop in one internode, fail to do so in the next, may or may not develop in the next, and so on. A couple of examples may be given. Counting the internodes back from the apex, one never finds any trace of medullary vascular tissue in the first and second internodes (the apical meristem, being above the first node, is of course not counted). The central bundle normally develops in the third internode, and it may be developed in all of the nodes below this. An abnormal seedling of the ninth stage shows the bundle developed only in the seventh internode from the top, being entirely absent elsewhere. An abnormal seventeenth-stage seedling (near the end of the first growing season) shows the central bundle only in the third, fourth, fifth, seventh, eighth, twelfth, thirteenth, and fifteenth internodes.

Abnormalities in the peripheral bundles are less common. The failure of a side bundle to fork at the bottom of the internode has already been mentioned. In a single case of a mature seedling, another type of abnormality was found. In one of the basal internodes, the forks of one of the side bundles, undoubtedly normal in its younger state, had grown together at the base, owing to the large amount of secondary thickening. In the upper part of the internode there is a single bundle which forks normally, the forks coming together, however, at the base, the endodermis disappearing between them. As the leaf trace enters, the endodermis opens upon the outside and forms a complete sheath around the trace and the fused bundle, the latter opening just enough to allow the trace to be inserted between its halves.

In the basal internodes of the branches, there are usually four peripheral bundles. Rarely, however, one of the side bundles fails to be differentiated.

The mature plant

At the close of the growing season, the rhizomes produced at the base of the seedlings have developed the mature type of structure in their younger internodes. Growth now practically ceases, the

main axis of the seedling dying down. At the beginning of the next growing season, the growth of the plant is continued by the rhizomes, the apices of these turning upward as they grow, to form the aerial shoots, each internode of which contains one central and six peripheral bundles, each surrounded by a complete endodermis. The development of these internodal structures is exactly that which has been described for the seedling.

Passing back from the apex (see diagram, fig. 2), one finds at the second node a vascular ring, which just below the node breaks immediately into six bundles. As in the seedling, there is no differentiation of a sheath in this (second) internode. In the next node, however, a sheath appears, surrounding the vascular ring. Below this the sheath sinks in around the six peripheral bundles. An irregular sheath also appears around the central bundle, which first shows in this (third) internode. The internal endodermis passes through the next node in the manner already described in an old node of the seedling (figs. 3–8).

A cambium develops in the pair of bundles entering the stem from the leaves in the second internode from the apex. It appears in the side bundles in the next lower one. This cambium at first forms an incomplete ring, but in the older internodes it is frequently complete. The concentric structure thus produced, of pith surrounded by xylem, phloem, and a stereomatic pericycle, the whole surrounded by a sharply differentiated endodermis, certainly justifies HOLM'S statement (**5**, p. 309) that "in *Dianthera* the steles are very distinct and readily to be recognized as such, since they are cylindric and possess all the necessary elements."

The central bundle in the mature plant is plainly derived from vascular tissue passing downward from the four side bundles (figs. 2–7). As in the seedling, it arises first in the third internode, cambium usually showing in the fourth. The mature central bundle, as HOLM has described, usually has the appearance of being double, the mestome forming two arches, with parenchyma between, the whole surrounded by a well marked endodermal sheath.

The mature type of vascular structure seems to be rather constant. HOLM mentions that the central bundle may sometimes be lacking, but an examination of several hundred internodes of mature plants has failed to show such a condition. One single

internode, lying between two normal ones, showed three medullary bundles, the central one like the one ordinarily found, one a collateral bundle surrounded by an endodermis in structure therefore like one of the peripheral meristeles. The third, also surrounded by an endodermis, was a strictly concentric bundle, with no parenchymatous tissue, the protoxylem in the center, surrounded by a complete ring of xylem, cambium, and phloem.

The anastomosing of the bundles in the mature plant has already been described (fig. 1). Sections show that the minute vascular structure is very similar to that found in an old node of the seedling. Frequently, however, there is more of the inversely oriented vascular tissue. Some of the vascular elements on the sides of all six of the peripheral bundles may pass around to the inner face just before entering the node, and so become inverted.

HOLM, in speaking of the node, says (**5,** p. 323) "from the union of these steles each of the two opposite leaves receives three mestome cylinders, readily observed in the petiole as one central, very broad, and arch-shaped cylinder, with a much smaller one on either side." From the anastomosing bundles there is given off only one single trace to each of the leaves. This single trace, however, while passing through the cortex, gives off a branch on each side, so that each petiole does receive the three bundles as described by HOLM. This giving off of a single leaf trace, which trifurcates while yet in the cortex, is, according to VAN TIEGHEM (**11**), the conformation found in all of the Acanthaceae. It should be noted, however, that DEBARY (**3,** p. 243), in speaking of the course of the bundles in the stem, places *Ruellia maculata* in the group described as having "leaves opposite: traces of three or four bundles, which unite at the second lower node with those of the next lower pair: not pectinated."

The leaves of the aerial shoot have already been fully described by HOLM. In structure they are identical with those of the seedling, hence the correction concerning the presence of the marginal strand of collenchyma in the blade has to be made here also.

The axillary buds of the mature plant

As in the seedling, a bud is usually formed in the axil of each leaf. Those at the base of the aerial shoot usually develop into rhizomes, or more rarely into vertical aerial branches. In either

case, the development is exactly the same as in the buds of the seedling, having therefore an astelic structure. Each internode has six peripheral and one central bundle, except the basal, in which the central bundle may or may not be differentiated.

The buds of the upper part of the plant, on the other hand, ordinarily develop into inflorescence axes. As HOLM has pointed out, these have a monostelic structure (fig. 36). These buds start their development in the same way as do the buds which develop the rhizomes and stem branches. The first pair of leaves, or rather bracts, first furnish a pair of traces, then the pair of forked bundles develop; the second pair of bracts supply a pair of traces, exactly as in the other kind of bud. The connections of these bundles with each other and with those of the stem on which they are inserted are also as in the branch bud. The pedicel of the single flower developed in the axil of each bract possesses a ring of vascular tissue. At the base this ring splits on the face nearest the bract on one side, and nearest the inflorescence axis on the other. The two halves so produced become inserted between the bract trace and the forked bundle of the inflorescence axis.

The difference between the structure of the inflorescence axis buds and those forming ordinary branches soon becomes visible. One difference is the greater length of the internodes of the latter. The most important difference between them, however, lies in the fact that in the inflorescence axis, the inner layer of the cortex, while forming a rather irregular sheath around the stele, apparently never forms a strongly developed endodermis. This sheath, on passing out of a node, never sinks in between the bundles, but remains as a ring, marking the boundary, rather indistinct at times, between the cortex and the central cylinder. The parenchymatous tissue of the latter differs from that of the former in being made up of larger cells, and in containing a very much smaller proportion of air space. The general appearance of a cross-section is very similar to a monostelic stem in which the individual bundles tend to remain separate.

Let us now compare the insertion of a well developed branch with that of an inflorescence axis. Taking a case where the basal internode has no central bundle, we find that the trace of the subtending leaf enters between the abaxial side bundles of the branch.

The endodermal sheaths of the six branch bundles open up, each connecting with that of the adjacent bundles, so as to form a complete sheath around the leaf trace and the six branch bundles (figs. 33–35). Where the central bundle is present, a connection is made between the two pairs of side bundles and the central bundle, all of the vascular tissue of the latter passing to the periphery and becoming normally oriented. Then the ring of the six peripheral bundles and the incoming leaf trace become surrounded as before by a common sheath (figs. 37–41).

In the case of the inflorescence axis, the vascular ring shows a tendency to break up into six bundles. This ring opens on the side to allow the entrance of the leaf trace, or rather bract trace; the sheath then surrounds the ring and the trace (figs. 42–45). The structure so produced is in cross-section almost identical with that produced by the branch. The further history is the same for both types.

The organogeny of the flower

The apex of the inflorescence axis continues its activity all through the flowering season, giving rise to opposite, decussate bracts, in the axils of which are produced the flowers. The greatest growth of the inflorescence axis is due to intercalary activity in the basal internode.

In the axil of each developing bract a slight mound develops. On this mound, which is to be the flower, there appear first of all, apparently synchronously, the five sepals (fig. 46), followed very soon by the five petals. At first the latter are separate, but soon coalesce to form the corolla tube. About the same time that the corolla is initiated, two large mounds appear, marking the primordia of the stamens (figs. 47 and 48). There is never any trace of more than two stamens (five occur in some of the Acanthaceae, in other genera there are two stamens and three staminodia). The ovary grows up as a ring (fig. 49), the sides nearest and farthest from the axis of the plant being slightly (10–15 μ) higher (fig. 50). The petals soon coalesce, the stamens being carried up on the corolla tube. The ovarian "ring" closes in over the top and continues its growth to form the pistil with its deeply two-lobed stigma. The placentae grow out from the opposite walls of the ovary, near its base. Two ovules arise on each placenta. The two placentae now gradually

grow together, dividing the ovary into two cells. One ovule from each placenta is left in each cell.

The vascular supply of the floral organs

In the pedicel of a mature flower is to be found a complete ring of vascular tissue. Above this ring breaks up into 26 bundles, three of which pass out to each of the five sepals, five bundles passing up into the tube of the corolla, two large concentric bundles supply the stamens, and four pass up into the ovary. Two of the latter bundles, lying in the sagittal plane of the flower, pass up the carpellary walls, each giving off two laterals. The laterals die off near the top of the carpel, the medians however passing out into the style, which therefore possesses two bundles. The two remaining carpellary bundles branch, each giving off a bundle which supplies the placental wall. The other arm of each forks, the bundles so produced passing up the side walls of the carpel until near the top, where they disappear. Each of the five bundles passing out into the tube of the corolla gives off several branches while passing through the tube. Each of the stamen bundles pass up between two of the bundles of the corolla, being sharply distinguished from them in being concentric instead of collateral. They pass out into the stamens when the latter become free from the corolla tube.

As we pass down the short pedicel to its insertion, we find the ring first opens on the inner face (figs. 51 and 52). The inflorescence axis shows two large flat bundles, each of which now forks (figs. 51 and 52), each of the arms becoming applied to the sides of the opened ring from the pedicel (fig. 53). These two vascular masses then divide to allow the entrance of the single bract trace. The two vascular bundles now tend to round up (fig. 54). In the basal internode this division into two parts is not so marked, as the endodermal sheath usually forms a complete ring around the vascular tissue (fig. 36).

Discussion

According to HOLM, some of the species of *Dianthera* which he examined were monostelic. These were *D. comata* L., *D. glabra* B. & H., *D. inserta* Brandg., *D. ovata* Walt., *D. parvifolia* B. & H.,

D. pectoralis Murr., and *D. sessilis* Gray. I was unable to obtain any of these species for comparison. I did obtain seeds, however, of the fairly closely related *Justicia ventricosa*. A few of these germinated, and I was able to study a few of the seedling stages. The germination is similar to that described for *Dianthera americana*. Likewise are the first three stages. After that, the interfascicular cambium masks the primary structure.

Comparing this then with *Dianthera americana*, we find that they are at first exactly the same. The first point of difference is the failure of the interfascicular cambium to appear. This leaves the bundles separate, around which the endodermis turns in and surrounds, instead of remaining as a complete ring, as in *Justicia*.

In the mature plant, we find that the first two apical nodes of *Dianthera americana* are similar to other acanthaceous plants (*Justicia*, *Fittonia*, etc.). In the latter, the traces of the first pair of leaves pass down to a ring of vascular tissue. Below this node there are two arcs of tissue, each of which is evidently of three parts, showing three widely separated protoxylems. This internode, therefore, has a structure exactly like that of a young internode of the inflorescence axis of *Dianthera americana*. At the next node the opposite leaf traces enter between the two arcs. Below this node the original structure cannot well be made out, owing to secondary thickening.

It is evident that the seedling and the inflorescence axis of *Dianthera americana* show the primitive condition of the group, and that the formation of endodermal sheaths around each of the separate bundles, that is, the condition of astely, is a secondary condition, found only in a part of the species of *Dianthera* (according to Holm, *D. crassifolia* Chapm. and *D. lanceolata* Small, are also "polystelic").

Although astely apparently has not been previously described as occurring in the Acanthaceae, yet many other vascular abnormalities are known. The interxylary phloem of *Thunbergia* and others is well known. Intraxylary phloem (*Thunbergia*, *Hexacentris*, *Barleria*, etc.), medullary phloem (petiole of *Acanthus mollis*), and even medullary bundles (*Acanthus spinosus*, etc.), have also been described. It is thus seen that the family shows irregularities of vascular structure.

In *Dianthera americana*, the two chief types of abnormality found in the family occur, that is, the astelic condition and the medullary vascular tissue. The former is evidently not in any way dependent on the latter, since in the seedling the plant is frequently astelic when there is no medullary tissue developed.

In the terms of the stelar theory, *Dianthera americana* in its early stages is monostelic. In the young seedling the first endodermis differentiated, surrounding the nodal ring, corresponds to the inner layer of the cortex. The stem apex is rather broad and flat, but the three histogen layers of HANSTEIN can usually be made out. From the plerome is developed a central cylinder, all that is within the endodermis. The parenchyma of this stele corresponds, therefore, to pith and medullary rays.

This seems clear enough in the early stages of *Dianthera* and also in *Justicia*. In the latter this condition persists permanently; there is always a well marked cortex and central cylinder, with its pith. In the internode of *Dianthera americana*, on the other hand, an endodermal sheath about each bundle is initiated, passing around the bundle and inclosing on the inner face of the latter a mass of parenchyma. From our previous interpretation, this endodermis differentiates on the sides of the bundles from the parenchymatous cells of the medullary rays, and on the inner face from the pith itself. In such a case the endodermis surely cannot correspond with any morphological layer.

Now let us examine the fate of the parenchyma of the original central cylinder, that is, that derived from the plerome. That part which is inclosed within the endodermal sheath undergoes little change, while that outside the sheath gradually becomes so modified as to appear exactly the same as the cortical tissue. At this mature stage, then, there is no visible differentiation between the cortex and the pith, except within the endodermis. And yet we have seen that they had an entirely different origin, the one derived from the plerome, the other from the periblem. Unless one leaves out of account the different origin, and compares only the mature structures, one is certainly not justified in saying in this case, as VAN TIEGHEM and DULIOT (**12**, p. 275) say in their definition of astely, that the bundles are "directement plongés dans la masse

générale du corps qui ne se séparé pas alors en écorce et conjonctif" (p. 275).

STRASBURGER (9) distinguishes between the inner layer of the cortex, which is a morphological layer, and the endodermis, which is merely "an air-tight barrier which does not prevent the passage of water through its cells. Such a layer is found in a position to shut off the water-conducting system of a plant from its air-containing lacunar system, but this position may vary within the same genus, and has no necessary connection with any morphological region" (quotation from TANSLEY 10).

According to this interpretation of the endodermis, which is therefore merely a physiological layer, astely is merely a modification of monostely. This is the view already taken by STRASBURGER (9); the same idea is presented in a recent paper by GRÉGOIRE (4). The parenchyma of the central cylinder, that is, outside of the endodermis, becomes different from that inclosed within the sheath, owing to the different physiological environment, and it becomes, like the cortical tissue, a response to the same physiological conditions.

If we leave out of account for the present the surrounding endodermis, we see that the medullary system of *Dianthera americana* corresponds to what COL (1), in his work on the arrangement of bundles, calls "série M'." He defines this type as follows (p. 242): "faisceaux normaux rentrant dans la moelle de la tige. Ils s'accolent inférieurement à d'autres faisceaux medullaires, et tous ceux des entre-nœuds les plus inférieure de la tige se poursuivent et se terminent isolément dans la racine (dans le bois) ou à la base de la tige."

WEISS (14) has shown that all medullary bundles of the stem are foliar bundles. The work of LIGNIER (7), KRUCH (6), and COL (1, 2) fully confirms this. In *Dianthera americana* it is easy to follow the leaf trace downward through two internodes, and to see that a part then turns inward to form the medullary vascular tissue.

In a paper describing for the first time the medullary bundles of *Acanthus spinosus*, VESQUE (13) says that he thinks the primary effect of the internal position of the phloem is its very efficacious

protection. He calls attention to its common occurrence in lianes and in creeping plants, and says that the protection counterbalances the danger to the phloem due to the great length and weakness of the stem.

COL (**2**), on the other hand, presents the following hypothesis (translated from p. 275): "The histological structure of the conductive tissues does not permit a sufficient condensation to form a single circle. The wood becomes condensed, more easily than the phloem, into a small bundle; without doubt on account of the fluidity of the ascending sap, and of the easy passage of liquids from one vessel to another. For converse reasons, the phloem is less capable of becoming condensed." When two bundles come together, therefore, the phloem passes around the sides of the wood to the inner face, or it may even become medullary. While it is undoubtedly true that the phloem is better protected in its internal position, as suggested by VESQUE, yet from my observations on *Dianthera americana*, it would seem that the hypothesis of COL certainly holds in that plant.

It may be that, in this case, the internal vascular tissue is correlated with the lack of a complete ring of vascular tissue. The phloem, not finding sufficient room on the outer face of the individual bundles, becomes crowded around to the sides, or even to the inner face of the bundles. The new vascular tissue descending from the uppermost leaves does not find room for its insertion, so part of it at least passes inward to form the central bundle. After it has begun its development imbedded in the pith, a sheath finally differentiates to separate it from the air-containing tissue of the much modified mature pith.

As to the cause of the astelic conditions found in this and other species of *Dianthera*, very little can be said. It is probably correlated, however, with the aquatic habitat. The large amount of air space undoubtedly is to be correlated with the aquatic habitat. If we agree that the endodermis is not a morphological boundary, but a physiological layer separating the vascular tissue from the "air-containing lacunar system," as claimed by STRASBURGER, then we have a simple, plausible explanation of this phenomenon.

More comparative work on this and other species of *Dianthera*

is needed, however, especially to find out if possible the physiological value of the endodermis. Possibly such work would lead to the discovery of the reason why some species of this genus are monostelic, and apparently normal in every way, while other species are abnormal in being astelic, and in possessing medullary vascular tissue.

Summary

The mature plant of *Dianthera americana* is astelic, instead of polystelic, as claimed by Holm. It possesses six peripheral meristeles and one central medullary bundle, each completely surrounded by an endodermal sheath. At the nodes these anastomose.

The seedling is at first monostelic; the individual bundles gradually become surrounded by the endodermal sheaths.

The mature type of structure with six bundles is derived from the seedling type with only four, by the increase of the size of the leaf gaps.

The inflorescence axis is monostelic.

Dianthera americana differs from related forms in the lack of interfascicular cambium, the individual bundles becoming surrounded by endodermis. Its medullary bundle is quite comparable to the medullary bundles of *Acanthus spinosus*, many Campanulaceae, and other plants.

It is probable that astely is merely a phase of monostely, the endodermis being a physiological layer, the medullary and cortical parenchyma becoming similar owing to like physiological conditions.

Astely in this plant is probably correlated with its aquatic habitat.

Johns Hopkins University
Baltimore, Md.

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EXPLANATION OF PLATES I–IV

All drawings of sections were made by means of a camera lucida. In the diagrams, xylem is represented by cross-hatching, phloem by dots. In figs. 3–9 the endodermis is represented by cells. The index letters are as follows: *A.R.*, adventitious root; *B*, bract; *BR*, branch; *BR.T.*, branch trace; *C*, carpel; *C.B.* central bundle; *CL*, calyx; *COT*, cotyledon; *CR*, corolla; *END*, endodermis; *EP*, epidermis; *ESP*, endosperm; *I.A.*, inflorescence axis; *L*, leaf; *L.T.*, leaf trace; *M.PH.*, medullary phloem; *P.B.* peripheral bundle; *PC*, procambium; *PPH*, protophloem; *P.R.*, primary root; *PX*, protoxylem; *S*, stamen; *ST*, stem; *T*, testa; *T.A.*, transverse arm.

PLATE I

FIG. 1.—Reconstruction of the vascular system of two adjacent mature nodes.

FIG. 2.—Diagram of the paths of the peripheral bundles of a mature stem.

FIGS. 3–8.—Series of successive transverse sections through a mature node, passing from fig. 3, made just at the top of the node, to fig. 8, made just below the node; ×45.

FIG. 9.—Transverse section through the upper part of an internode of an old seedling, showing one central and four peripheral bundles; ×45.

FIG. 10.—Part of a sagittal section of a seed, directly opposite the micropyle, showing the testa with its thickened epidermal cells, and the endosperm of two layers; ×185.

FIG. 11.—Sagittal section of a seed; ×12.5.

FIG. 12.—Longitudinal section of a seed, made perpendicular to the plane of the section shown in fig. 11, and through the line *mn;* ×12.5.

PLATE II

FIG. 13.—Transverse section of the upper part of the hypocotyl of a ripe seed, just below the insertion of the cotyledons; ×185.

FIG. 14.—Transverse section through the middle portion of the same hypocotyl, showing the periclinal division of the endodermis on either side of the stele; ×185.

FIG. 15.—Habit sketch of a seedling, stage I, with cotyledons still inclosed within the testa; ×1.5.

FIG. 16.—Transverse section of the upper portion of a first-stage seedling, just below the insertion of the cotyledons, showing the two "double" cotyledonary traces; ×185.

FIG. 17.—Diagram of the paths of the bundles in a seedling, stage I.

FIG. 18.—Diagram of the paths of the bundles in a seedling, early phase of stage II.

FIG. 19.—Habit sketch of a seedling, stage II (late phase); ×1.

FIG. 20.—Diagram of the paths of the bundles in a seedling, late phase of stage II.

FIG. 21.—Diagram of the paths of the bundles in a seedling, early phase of stage III.

FIG. 22.—Habit sketch of a seedling, stage III; ×1.

FIG. 23.—Transverse section of one of the side bundles in the basal epicotylar internode of a third-stage seedling, showing its "double" appearance, the three protoxylem, and three protophloem elements; ×380.

FIG. 24.—Transverse section of the same bundle as shown in fig. 23, at a lower level, just at the top of the fork; ×380.

FIG. 25.—Transverse section of the same bundle still lower down, the forking complete; ×380.

FIG. 26.—Surface view of a glandular hair; ×380.

FIG. 27.—Longitudinal section of a glandular hair and neighboring epidermis; ×380.

FIG. 28.—Transverse section of the uppermost internode of a third-stage seedling, showing the two procambial bundles of the traces of the uppermost pair of leaves imbedded in the ground meristem; ×380.

FIG. 29.—Diagram of the paths of the peripheral bundles in a seventeenth-stage seedling (near end of growing season), showing the gradual development of the "mature" type by the increase in length of the leaf gaps.

PLATE III

FIG. 30.—Restoration of the vascular system of a node of a fourth-stage seedling, showing the courses and attachments of the intranodal medullary phloem strands.

FIG. 31.—Habit sketch of an old seedling (stage XVII), near end of growing season, showing the development of rhizomes from the basal axillary buds; ×0.5.

FIG. 32.—Transverse section of the margin of the blade of a mature leaf, showing the collenchymatous strand; ×210.

FIGS. 33–35.—Series of successive transverse sections through the upper part of a node, showing the insertion of a branch which has no central bundle developed in its basal internode.

FIG. 36.—Transverse section of the stele of the basal internode of a mature inflorescence axis; ×45.

FIGS. 37–41.—Series of successive transverse sections through the upper part of a node, showing the insertion of a branch in which the central bundle has developed in the basal internode.

PLATE IV

FIGS. 42–45.—Series of successive transverse sections through the upper part of a node, showing the insertion of an inflorescence axis; ×50.

FIG. 46.—Longitudinal section through the apex of an inflorescence axis, showing the origin of the opposite bracts, the axillary flowers, and the primordia of the calyx on the lower flowers; ×50.

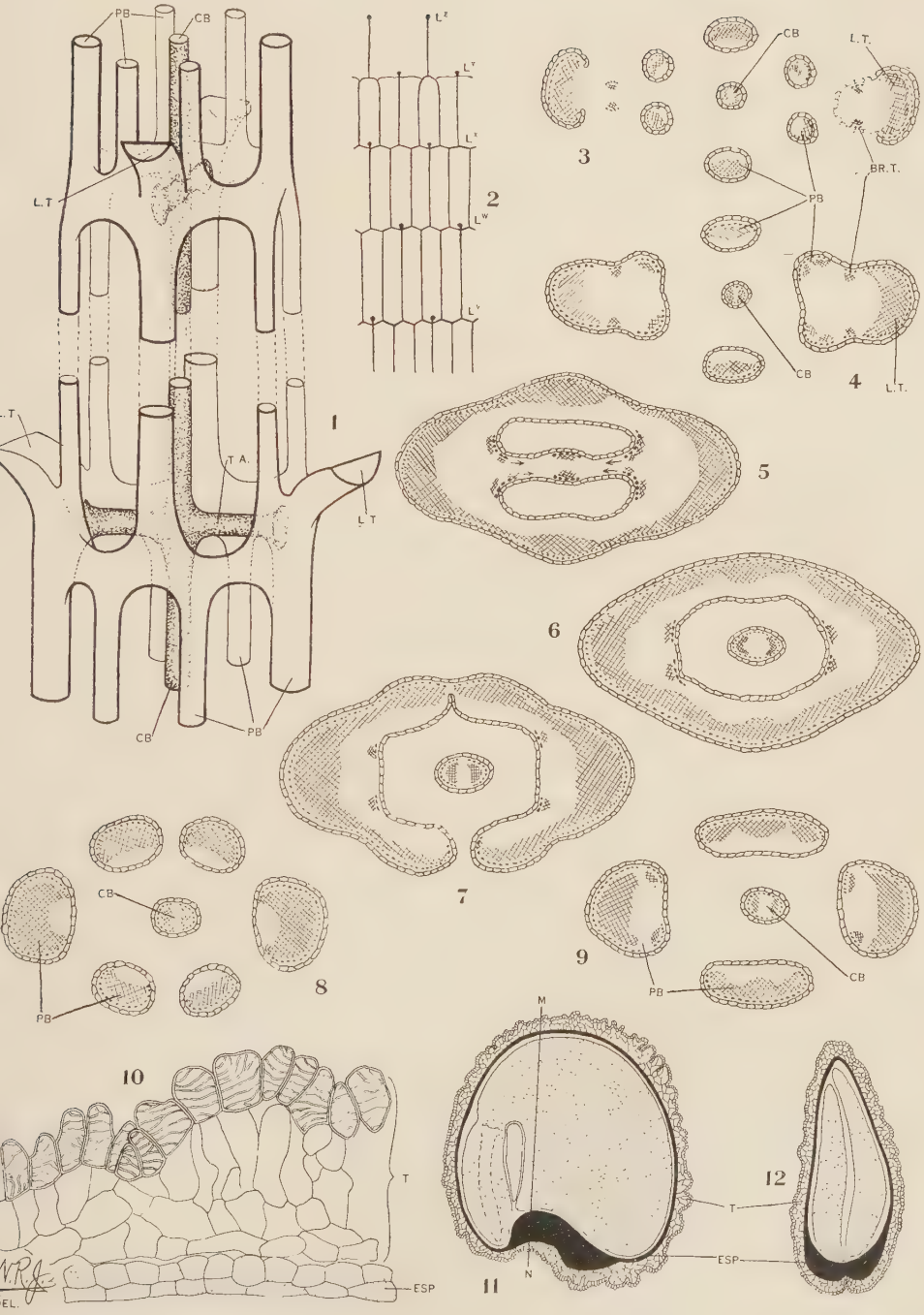
FIG. 47.—Longitudinal section of a young flower, not quite median, showing the bract, calyx, corolla, one of the stamens, and the edge of carpel; ×50.

FIG. 48.—Longitudinal section of a young flower, made perpendicular to that shown in fig. 47, along the line *mn*, showing the two large stamens free from the corolla; ×50.

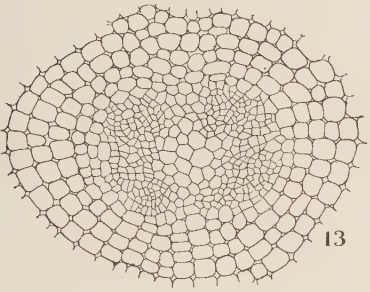
FIG. 49.—Sagittal section of a slightly older flower, showing the formation of the ovarian cavity; ×50.

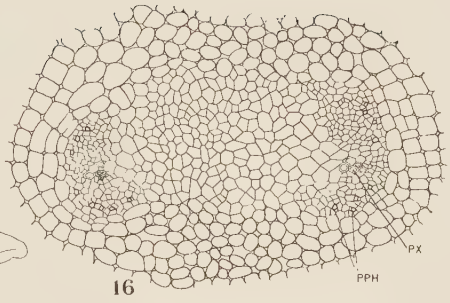
FIG. 50.—Transverse section (very slightly oblique) of a flower of about the same age as that shown in fig. 49, showing the arrangement of the floral parts, and the two lobes of the carpels; ×50.

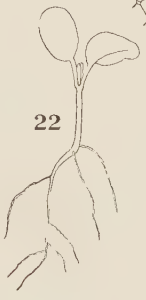
FIGS. 51–54.—Series of successive transverse sections through a node of an inflorescence axis, showing the insertion of the bundles of the opposite pedicels and bracts with those of the main axis; ×22.5.

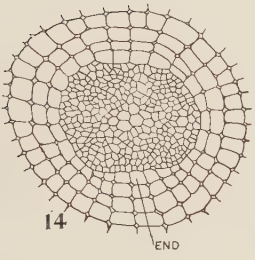


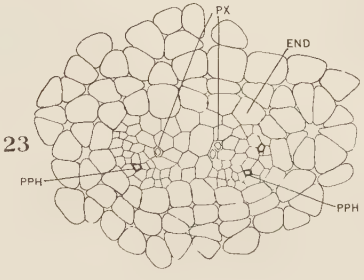
JONES on DIANTHERA

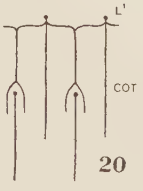


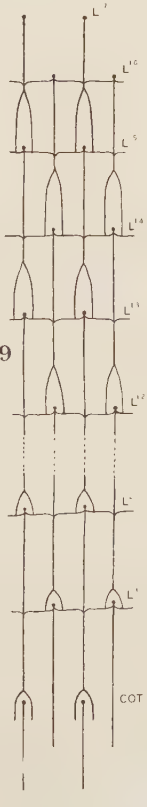


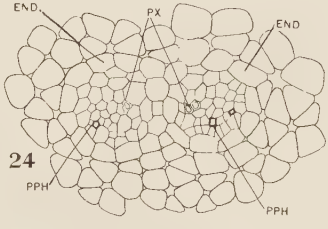


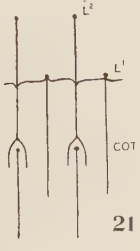


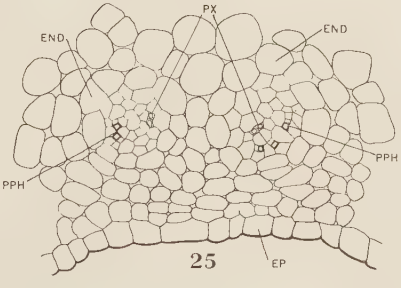


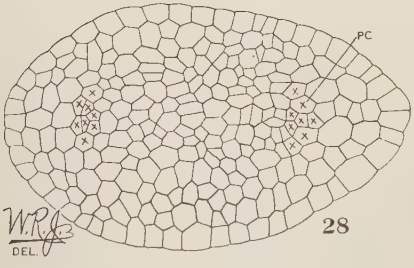












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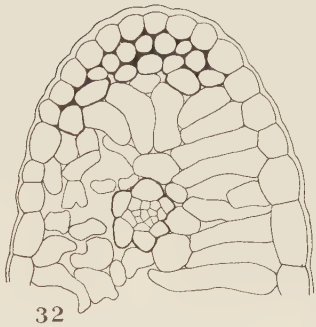

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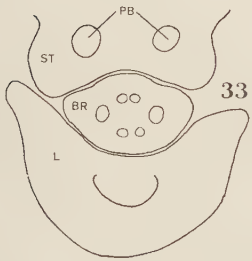

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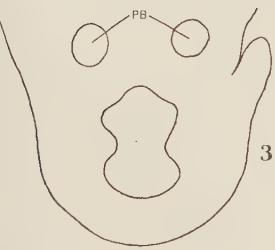

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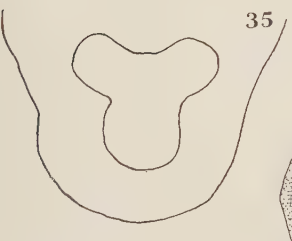

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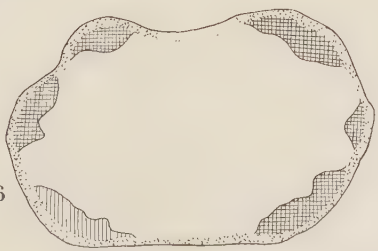

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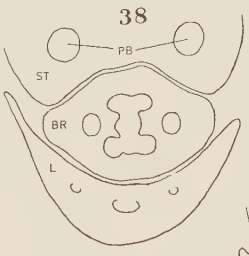

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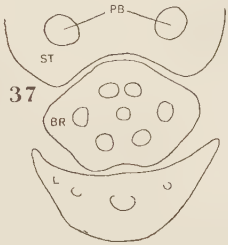

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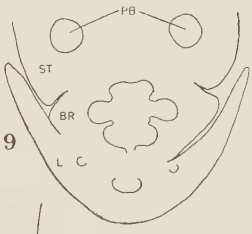

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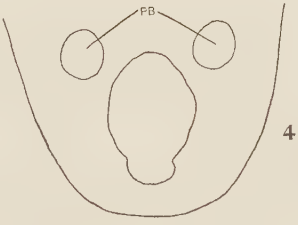

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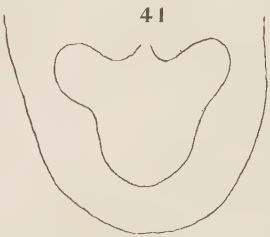

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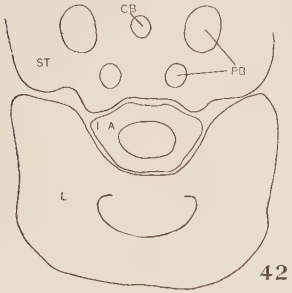

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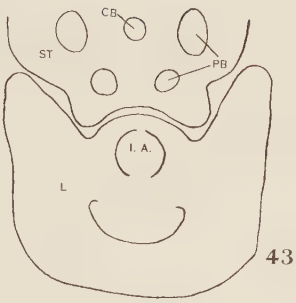

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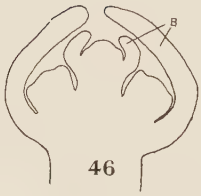

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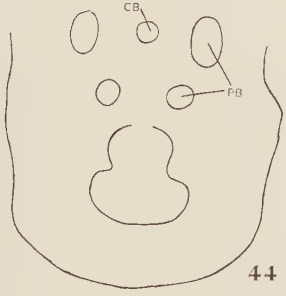

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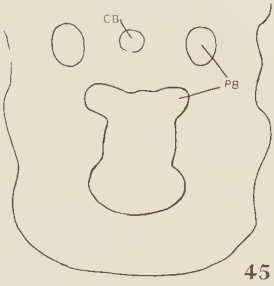

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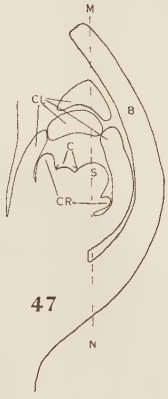

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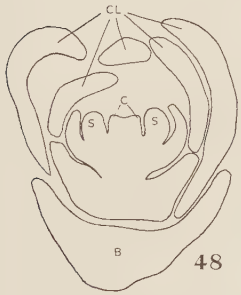

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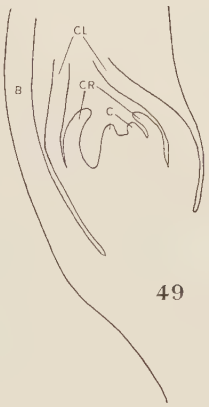

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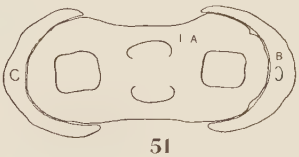

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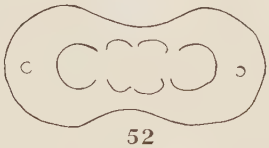

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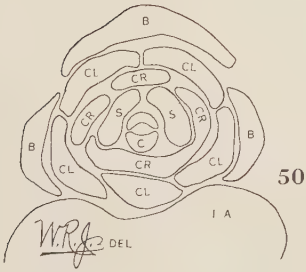

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VITA

The writer, William Ralph Jones, was born in Baltimore, Maryland, on June 16, 1883. His parents are William F. Jones and Emma Richardson Jones.

After having prepared at the Deichmann College Preparatory School, of Baltimore, he entered the collegiate department of the Johns Hopkins University, in October 1902, and in June 1906, received its degree of Bachelor of Arts. During the summer of 1906, he worked on the Maryland State Botanical Survey, under Dr. Forrest Shreve. During the school year of 1906–7, he taught botany and physiography in the Baltimore City College. He was Botanist to the Park Board of Baltimore City during the spring and summer of 1907. He taught biology and geology in the Louisiana Industrial Institute during the academic year of 1907–8. In October 1908, he entered the Johns Hopkins University, holding while there a University Scholarship the first two years, and an Assistantship the third year.